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THE HEREDITY OF ORANGE EYE COLOR IN DROSOPHILA MELANOGASTER[1]

THERE are three points of special interest in the heredity of orange eye color. First, the eye color is due to the presence of two sex-linked genes; second, these two genes may separate in the F_1 female when orange is crossed to the wild stock, producing in F_2, in addition to orange and wild type males, a third eye color called salmon[2]; third, when an orange male is crossed to the parent stock, reduced, only orange and wild type males appear in F_2.

Orange first appeared in the sixth generation of the plus selected line of the mutant strain reduced. Eleven males appeared from a single pair of parents. Several of these males (orange reduced) were mated to wild type females. All F_1 flies had red eyes. Twenty-seven F_1 pairs were mated (Table I). Of the F_2 males 850 were wild type (red-eyed), 785 were orange reduced, 585 were reduced, 586 salmon, 15 orange, and 6 salmon reduced. This behavior led us to suspect that orange

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[1] Contribution No. 182.

[2] Since this paper went to press Professor Morgan kindly sent us some stock of garnet. The crosses show salmon and garnet to be the same.

TABLE I

F_1 ♀ Wild Type × F_1 ♂ Wild Type (from Orange Reduced ♂ × Wild Type ♀)

Bottle Number	Female	Male					
	Wild Type	Wild Type	Reduced	Orange Reduced	Salmon	Orange	Salmon
789....	194	65	42	61	46		
798....	127	31	22	33	34		
804....	92	15	19	30	11		
808....	109	26	24	29	30	2	
814....	72	17	9	14	13		
815....	140	33	23	30	16	2	
816....	123	22	16	25	14		
831....	65	17	8	12	7		
854....	77	30	11	14	9		
859....	69	18	11	13	15	1	
860....	66	18	13	22	13		
1,431....	100	30	13	25	17	1	
1,372....	174	48	39	31	31		
1,494....	28	12	7	8	5		
1,495....	173	45	34	37	30	1	
1,557....	149	31	25	42	22	1	
1,569....	112	87	25	29	19	2	2
1,570....	106	20	20	17	17	1	
1,571....	66	22	9	10	15		
1,674....	111	26	27	27	33		
1,751....	175	62	41	55	42	1	1
1,736....	207	64	27	72	26		
1,724....	174	55	21	36	24	1	
1,720....	158	35	30	40	34	1	
1,441....	111	39	27	32	21		1
2,431....	74	22	20	22	19	1	
2,433....	81	20	22	19	23		2
Totals...	3,133	850	585	785	586	15	6

TABLE II

F_1 × F_1 [from ♂ Salmon × ♀ Wild Type (from Stock)]

Bottle Number	Female	Male	
	Wild Type	Wild Type	Salmon
1,612......	146	65	54
1,665......	123	51	34
1,668......	175	69	68
1,679......	121	69	54
1,682......	130	68	54
1,689......	161	63	56
1,701......	117	54	62
Totals...	963	439	382

eye color was due to the presence of two sex-linked genes, one of which by itself produced no visible effect, but when the two were brought together orange was the result. With this hypothesis in mind we attempted to prove or disprove it and believe we have demonstrated that the suggested explanation is the correct one.

First, some of the F_2 salmon males were mated to wild and the eye color shown to be due to a single sex-linked gene. An examination of the F_2 males when an orange reduced male is mated to a wild female (Table I), shows that practically all salmon males (586 out of 592) are wild type with respect to bristle number, and that practically all orange males (585 out of 600) are reduced. These results showed that the modifying gene which changes salmon into orange is closely linked to reduced. Most of the F_2 reduced red-eyed males then should carry this modifier and we should be able to produce orange flies in the second generation by mating these reduced F_2 males to salmon females. Such crosses have been made and the results show that the F_2 reduced males do carry such a gene which when added to salmon produces orange. The two genes for salmon and salmon modifier are brought together in the same chromosome by crossing over in the F_1 female (Table III).

TABLE III

(*a*) REDUCED ♂ (F_2 FROM ORANGE REDUCED ♂ × WILD ♀) × SALMON ♀

Wild type ♀	Salmon ♂
966	823

(*b*) F_1♀ [FROM (*a*)] × ORANGE ♂ FROM STOCK

Bottle Number	Female			Male		
	Wild Type	Salmon	Orange	Wild Type	Salmon	Orange
260.....	233	66	134	248	117	116
261.....	102	49	62	85	44	47
262.....	157	52	94	184	74	61
263.....	69	23	38	63	42	29
266.....	45	20	34	54	23	24
Totals ..	606	210	362	634	300	277

That the modifying gene lies in the X chromosome rather than in one of the autosomes is clearly shown by the F_2 ratios when orange is mated to a wild female. If the gene were reces-

TABLE IV

F_1 ♀ WILD TYPE × F_1 ♂ REDUCED (FROM SALMON ♂ × REDUCED ♀)

Bottle Number	Female		Male					
	Wild Type	Reduced	Wild Type	Reduced	Salmon	Salmon Reduced	Orange Reduced	Orange
8,347....	133	112	60	76	72	4	43	1
8,348....	124	119	46	57	67		40	3
8,354....	88	105	47	43	80	4	47	
Totals ..	345	336	153	176	219	8	130	4

sive and in an autosome all the F_2 females should be wild type. Such is the case. Of the F_2 males, four should be red-eyed, three salmon, and one orange. If the gene were dominant, the ratios among the males should be four red, one salmon, and three orange. The actual results are given in Table I. We find neither of the former ratios, but 1435 red-eyed, 800 orange, and 592 salmon. The fact that there is a linkage between the genes for salmon modifier and reduced is further evidence that the gene for salmon modifier is in the X chromosome.

Orange eye color, then, is due to two sex-linked genes, one of which when alone produces salmon; the other called salmon modifier, when alone produces no visible effect, but when added to salmon produces orange. The discovery of such a modifying gene is not new as Bridges has demonstrated seven of them which modify eosin eye color. It does lend support, however, to the presence and behavior of such genes.

These same orange reduced males when mated to reduced females give a very different result from the cross to the wild. When crossed to reduced, orange behaves as a single sex-linked character (Table II). Why this difference? At first it was our impression that the reduced strain carried a non-crossover factor. This was disproved, however, by mating reduced to other sex-linked characters. The other alternative and the correct interpretation we think, is that the reduced strain is homozygous for the gene for salmon modifier. This is easily demonstrated by mating salmon to the reduced line. If the reduced line carries the gene for salmon modifier, then a cross of this line to salmon should give some orange males in F_2. Such is the case (Table IV). The reduced strain, then, carried the gene for salmon modifier before the gene for salmon appeared.

No attempt has been made to locate accurately the genes for reduced, salmon, and salmon modifier. Sufficient crosses have been made, however, to approximate their positions, which are as follows: reduced, 5.24; salmon modifier, 5.94; salmon, 41.33.

DESCRIPTION OF TABLES

Table I gives the results of mating the F_1 flies produced by crossing an orange reduced male to a wild type female. All the F_2 females are wild type. Of the F_2 males 850 are wild type, 585 reduced, 785 orange reduced, 586 salmon, 15 orange, and 6 salmon reduced.

Table II gives the F_2 results of mating a salmon male to a wild type female. Of the males 439 were wild type and 382 salmon.

Table III (*a*) and (*b*), gives (*a*) the results of crossing an F_2 reduced male (from an orange reduced male × a wild female) to a salmon female. The females are wild type and the males salmon. In (*b*) the F_1 wild type females were mated to orange males. The orange males were used instead of the salmon to bring out orange in the females. Orange males and females appear. Hence the F_2 reduced males must have carried the gene for salmon modifier.

Table IV gives the F_2 results of crossing a salmon male to a reduced female. Orange males appear. Hence the reduced line must be homozygous for salmon modifier.

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AN APPARATUS FOR MICRODISSECTION

To secure the greatest accuracy in the control of needles for cell dissection an apparatus has been devised on the following plan. The needle is attached to a right angled triangular plate (Fig. *A*), each corner of which is moved by a milled headed screw. The working of any screw causes the movement of the plate about a line through the points of the other two screws as an axis, thus producing motion of the needle point in the three planes of space by manipulation of the screw heads. The nature of the bearings of the screw points on the plate eliminates all side play. The conical end of one screw works into a circular